Vegetative and floral phenology of the mangrove, *Ceriops tagal*, with observations on the reproductive behaviour of *Lumnitzera racemosa*, in the Mgeni Estuary

T.D. Steinke* and A. Rajh

Marine Science Unit, University of Durban-Westville, Private Bag X54001, Durban, 4000 Republic of South Africa

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Phenological observations were conducted on *Ceriops tagal* Perr. C.B. Robinson (vegetative and floral) and *Lumnitzera racemosa* Willd. (floral) in the Mgeni Estuary. Leaf emergence in *C. tagal* was unimodal with high initial values in early summer (December), followed by decreasing numbers of leaves for the remainder of the summer, with the last leaves making their appearance in June/July. Leaf abscision showed high values in August/September but, with the exception of smaller peaks in April, produced no other consistent trends. Leaf/shoot ratios revealed an undulating pattern with high values in summer and decreasing values in the cooler months. Mean longevity of leaves marked in the first two years of the study was approximately 30 and 32 months respectively. It was not possible to follow reproductive behaviour in *C. tagal*. In *L. racemosa* a period of 3–4 months was required for development from flowers to the abscission of propagules. The significance of these results for litter production is discussed.

Waarnemings is op die vegetatiewe en blomfenologie van *Ceriops tagal* Perr. C.B. Robinson en die blomfenologie van *Lumnitzera racemosa* Willd. in die Mgeni-riviermond gemaak. Blaarverskyning in *C. tagal* was unimodaal met hoër aanvanklike waardes in die vroeë somer (Desember) gevolg deur minder nuwe blare gedurende die res van die somer tot in Junie/Julie. Daar was 'n groot mate van blaarafsnyding gedurende Augustus/September, maar, met die uitsondering van 'n kleiner piek in April, was daar geen ander konsekwente neigings nie. Blaar/loot verhoudings het gewissel, met hoër waardes in die somer en laer waardes in die koeler maande. Die lewensduur van blare wat gedurende die eerste twee jaar van die studie gemerk is, was ongeveer 30 en 32 maande respektiewelik. Dit was nie moontlik om die voortplanting van *C. tagal* te bepaal nie. In *L. racemosa* het dit 3–4 maande geneem van blomontwikkeling tot die afsnyding van die propagules. Die implikasies van hierdie resultate vir die vorming van plantafval word bespreek.

Keywords: Leaf abscission, leaf emergence, mangroves, reproduction.

*To whom correspondence should be addressed.

Introduction

After the independence of Mozambique in 1974 there were fears that a security risk situation might arise in the north-eastern corner of South Africa. This area includes the Kosi system (26°55'S) which has six species of mangroves, two of which, namely, *Ceriops tagal* Perr. C.B. Robinson and *Lumnitzera racemosa* Willd., do not occur naturally further south (Ward *et al.* 1986). As a deterioration of the security situation would have made visits to the Kosi system extremely difficult and thereby virtually precluded any local research on these two species, it was decided to establish a limited number of these mangroves in the Durban area. Propagules of these species were, therefore, planted in pots in a glasshouse at the University of Durban-Westville and thereafter transplanted into the field when approximately 200-mm tall, in situations similar to their natural habitat, at the Beachwood Mangroves Nature Reserve (Mgeni Estuary) (29°48'S). The transplants have been monitored regularly, and relatively frequent observations on the naturally occurring trees in the Kosi system have suggested that the transplants are exhibiting a similar growth pattern (Ward *et al.* 1986). As part of the monitoring process and to provide more information on growth patterns which could serve as a basis for further research, the present study on the phenology of *C. tagal* and *L. racemosa* was conducted.

Materials and Methods

The study was initiated on 19 May 1988 and continued until 20 October 1993, a period of approximately 5.5 years. The experimental trees of *C. tagal* varied in height from 1 to 2 m, the tallest were in exposed situations and were fertile. Leaves on a total of 32 shoots from five trees were marked. The marked shoots were chosen at random and included those from the base to the top of the trees, although most marking was conducted at a height of approximately 1 m. Marking was done lightly with a Koki pen on the adaxial surface after preliminary observations had shown that this method had no damaging effects on the heavily cuticularized leaf surfaces (Steinke 1988).

After the initial marking, the trees were visited at 4-weekly intervals, except during the period 7 December 1988 to 18 January 1989 when the normal pattern of observation was unavoidably disrupted. After 5 May 1993, no new leaves were marked and observations were carried out until 20 October 1993 to record only the abscission of the last of the leaves marked during 1989/90. At each visit, observations were made on the emergence of new leaves and flower buds and the abscission of senescent leaves and reproductive material on each shoot. New leaves were marked as soon as they had unfolded. Each year of the study runs from June to May.

For each observation date mean values for leaf emergence, leaf abscission and leaf/shoot ratios were calculated, and the data on the first two were subjected to analysis of variance and, where appropriate, to correlation and regression analysis (Rayner 1969). Meteorological data used for calculating correlations with these data were obtained from S.A. Weather Bureau, Louis Botha Airport, Durban.

As the number of trees of *Lumnitzera racemosa* established at Beachwood was considered too low for more detailed recordings, observations were limited to the reproductive state of the trees on each of the marking dates for *C. tagal*. The experimental trees were at least 1 m in height and were fertile when observations commenced coincidentally with those on *C. tagal*.

Results

Leaf emergence

The trends for leaf emergence are presented in Figure 1a. Leaf emergence was markedly unimodal with initial high values in early summer (December), followed by decreasing numbers of leaves for the rest of the summer, with the last new leaves making their appearance in June/July. No new leaves were recorded from late winter to early summer.

Analysis of variance revealed that the high leaf emergence which occurred in December was significantly different ($P < 0.01$) from that of all other months (Table 1). January produced the next highest rate of leaf emergence which was significantly different ($P < 0.05$) from the values for February to May, which were, however, not themselves significantly different from each other. The low values for June and July were not significantly different from those in the late growing season (April/May) or from those in late winter/spring (August to October). There was no significant difference in mean annual leaf emergence in the five years of the project. Leaf emergence was significantly correlated ($r = 0.81$, $P < 0.01$) with mean monthly temperatures. This high correlation was obtained because of the high values in the warmer months and low values in the cooler months. Clearly, the very high values in December, when mean temperatures were lower than in the succeeding three months, were not taken into account by this calculation. There was also a good correlation ($r = 0.96$, $P < 0.01$) between annual rainfall and leaf emergence (both calculated from July to June), suggesting that the appearance of new leaves was restricted in drought years.

Leaf abscission

The trends for leaf abscission are presented in Figure 1b. Leaf abscission showed high values in August/September but, with the exception of smaller peaks in April, produced no other consistent trends.

Mean leaf abscission was greatest in August, and the difference between the rates in August and September was significantly different only at the 5% level (Table 1). The value for April was significantly lower than those for August and September ($P < 0.01$), and it was significantly different only from the lowest value (February) at the 5% level, while it was not significantly different from the values for the remaining months, which among themselves were not significantly different.

There were no significant differences in mean leaf abscission in the different years of the study and no correlation between leaf abscission and temperature. However, the correlation between annual rainfall and leaf abscission (both calculated from July to June) was very nearly significant ($P < 0.05$), which suggests that leaf fall might be increased in drought years.

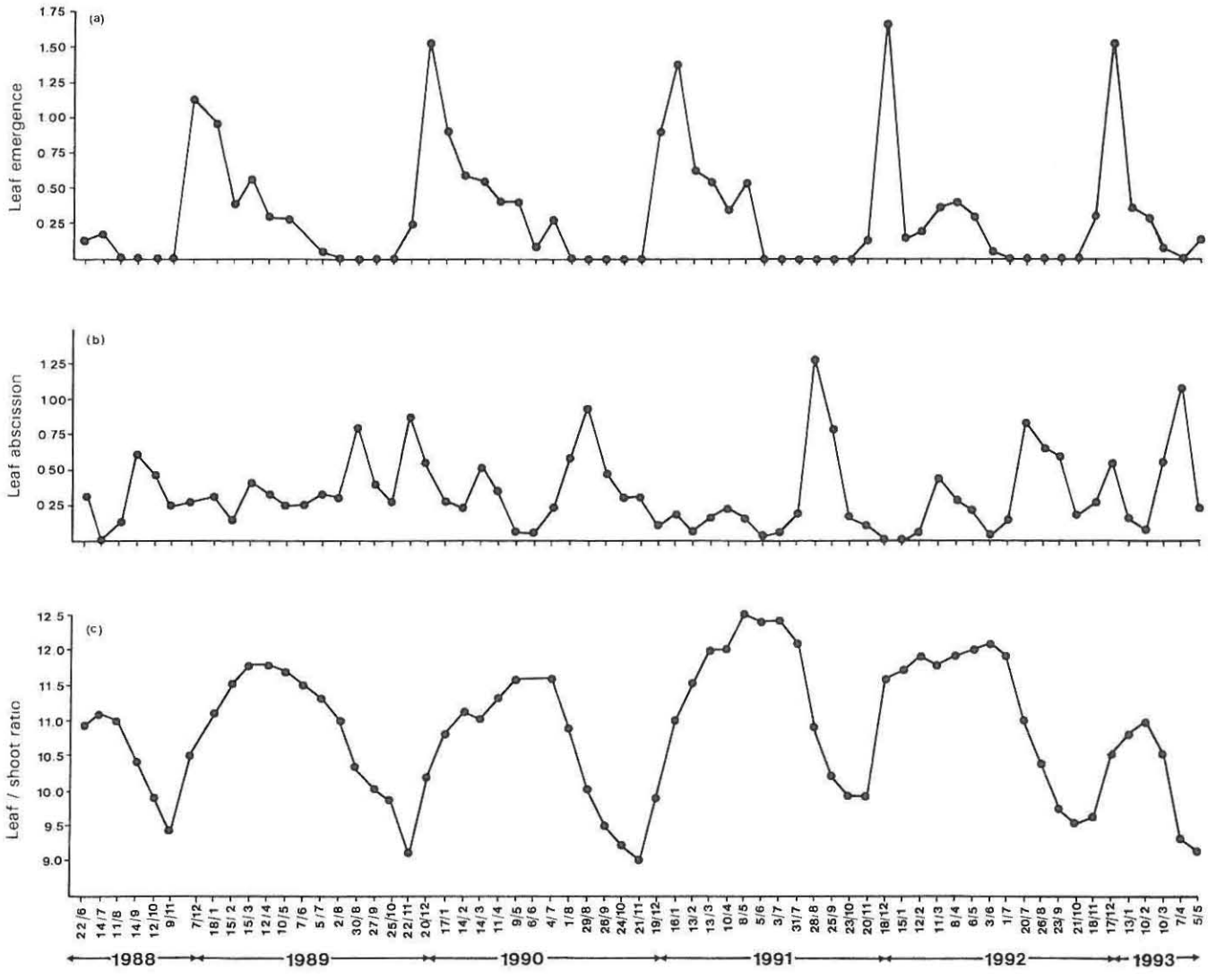

Figure 1 (a) Mean leaf emergence, (b) mean leaf abscission, and (c) mean leaf-shoot ratios, in *C. tagal* for the period 1988/89 to 1992/93.

Table 1 Mean monthly rates of leaf emergence and abscission (leaves/shoot/4-week period) in *C. tagal* for the period 1988/89 to 1992/93

Months	Dec	Jan	Feb	Mar	May	Apr	Nov	Jul	Jun	Aug	Sep	Oct
Leaf emergence	1.36 Aa	0.75 Bb	0.48 Bc	0.42 BCc	0.34 BCDcd	0.29 BCDcde	0.14 CDef	0.09 CDef	0.07 CDef	0.00 Df	0.00 Df	0.00 Df
Months	Aug	Sep	Apr	Mar	Jul	Nov	Dec	Oct	Jan	May	Jun	Feb
Leaf abscission	0.96 Aa	0.57 ABb	0.46 Bbc	0.43 Bbcd	0.36 Bbcd	0.35 Bbcd	0.29 Bbcd	0.27 Bbcd	0.19 Bcd	0.18 Bcd	0.14 Bcd	0.11 Bd

Any two treatments which do not have a letter in common differ significantly: capital letters denote significance at the 1% level, small letters show significance at the 5% level

Leaf/shoot ratios

Annual ratios showed a regular pattern of high values in the summer, reaching 12.5 leaves/shoot in 1991, followed by a decrease during the cooler months to the lowest value (between 9 and 10 leaves/shoot) in approximately November (Figure 1c).

Leaf longevity

It was possible to calculate longevity only for the leaves marked in 1988/89 and 1989/90, as most of those marked later had not abscised by the time observations were terminated. Leaves marked in the first and second years had a mean longevity of 896 and 953 days, or almost 30 and 32 months, respectively. The mean difference of 57 ± 61 days in favour of the second marking year was not significantly different.

There was a difference in longevity of leaves produced at different times within each year (Figure 2), i.e., a steady decrease in lifespan of leaves produced as the season progressed. The linear equation, $y = a + bx$, was fitted to these data (r values of −0.91 and −0.96 for the first and second years, respectively, highly significant, $P < 0.01$) and examination of the regression coefficients, b, in the above equation provided a basis of comparison of mean relative rates of decrease (Snedecor 1957). The b values were −46.6 and −35.6 for 1988/89 and 1989/90, respectively, indicating that the differences in longevity of leaves produced throughout the second year were not as marked as those in the first year.

Reproductive behaviour

Unfortunadely, the actions of vandals, who picked developing propagules before they were able to reach maturity, prevented a complete analysis of reproductive behaviour in *C. tagal*.

The main period of bud appearance was summer (January/February) with a lesser appearance in autumn (April/May). From bud appearance, the flowers and developing propagules were on the trees for a maximum period of 8 months before they disappeared.

On the other hand, it was possible to follow the reproductive process of *L. racemosa* from bud appearance to the abscission of fruit (Figure 3). The development period from flowering to the abscission of propagules was 3–4 months. The last flowers in June/July failed to develop into propagules.

Discussion

Although *C. tagal* is widely distributed throughout the Indo-Pacific region (Barth 1982), there is relatively little information on its growth and reproduction. This study, therefore, makes a contribution towards our knowledge of the species. Although it was conducted on material growing outside its known distribution range on the African continent, the close similarity between these data and those obtained in tropical Australia (Duke *et al.* 1984), as well as the apparent consistency of observations between Beachwood and the Kosi system, suggest that our results are valid.

The high values in the warmer months implied that temperature was an important factor determining leaf emergence in *C. tagal*. However, it is possible that these peaks were the result not only of higher temperatures but that other unmonitored factors might also have had an influence in the summer months, e.g. longer photoperiod, higher radiation intensity and more favourable soil moisture conditions during the rainy season. That temperature does play a significant role appears to be confirmed by the results obtained in tropical Australia (Duke *et al.* 1984) and Thailand (Wium-Andersen & Christensen 1978). In the former, mean winter temperatures are comparatively low and there is a

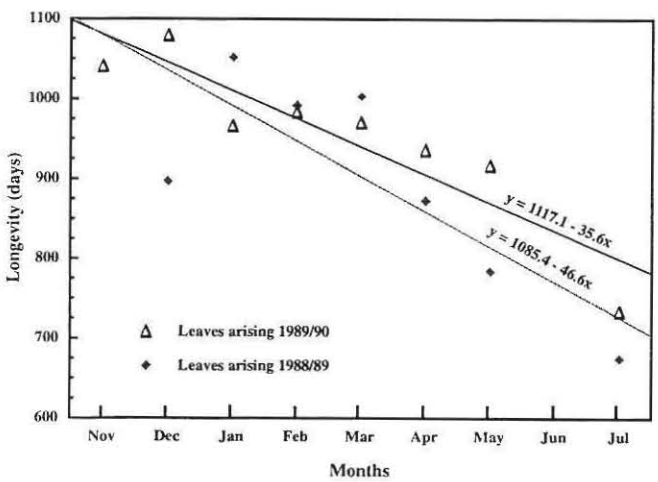

Figure 2 Mean longevity of leaves of *C. tagal* produced in 1988/89 and 1989/90.

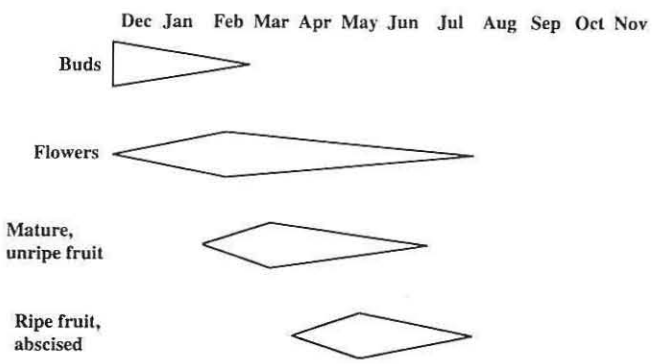

Figure 3 Reproductive development in *L. racemosa* from bud appearance to the abscission of fruit.

marked unimodal emergence pattern, whereas in Thailand, temperatures are more uniform and leaf production was sustained throughout the year. Saenger & Moverley (1985) found that in subtropical Queensland, although leaf production rates were low throughout the year, there was a slight seasonal increase in summer. However, their results indicated that *C. tagal* had the capacity to produce leaves at lower temperatures than were experienced in this study. The fact that even with increasing temperatures in spring/early summer there was no leaf production until December suggests that, in addition to temperature, there are other, possibly internal, factors that exert control over the onset and pattern of leafing in this country.

Although in this study leaf abscission occurred throughout the year, there was an increase during late winter/spring, which is the end of the dry period. At this time soil salinities rise, and then fall again with the onset of the rainy season (Naidoo 1989). Changes in ground-water salinity have been suggested as an important factor determining leaf fall (Pool *et al.* 1975), whereas Wium-Andersen & Christensen (1978) and Wium-Andersen (1981) related growth pattern to variations in ground-water salinity. They suggested that unimodal growth in mangroves is caused by strong seasonal patterns in ground-water salinity, whereas species exhibiting bimodal growth experience frequent tidal influence with consequently no prolonged changes in sediment-water salinities. As *C. tagal* is growing in an area which experiences only infrequent tidal inundations, marked seasonal changes in salinities can be expected. There is, therefore, a strong possibility that patterns of leaf emergence and abscission in this species are determined at least partly by this factor.

From Figures 1a and b, it is clear that the onset of leafing takes place only after the high rate of leaf abscission in early winter/spring. Previous work on *A. marina* (Steinke & Charles 1984) speculated hormonal involvement in controlling leaf abscission. If that should apply also to *C. tagal*, this suggests an internal mechanism which could also assist in regulating the burst of leaf emergence in December.

The patterns of leaf abscission and emergence were responsible for the undulatory curves of leaf/shoot ratios. These ratios reached their lowest value in October/November, between the late winter/spring peak in abscission and the December burst in leafing, and then increased sharply during early summer. The high summer values ensured that, at a period of high radiation intensity, shoots carried the greatest number of leaves, which would be advantageous to the trees. The maximum mean value of 12.5/1 approached the 3-month average of 13.4/1 reported by Duke *et al.* (1984) and individual shoots reached values of 20.0/1 for short periods. However, in 1992/93 the ratios did not attain the high values of the previous years as a result of a severe drought (rainfall approximately 50% of mean annual figure) which restricted leaf production and apparently increased leaf abscission.

Longevity of leaves varied from 22 to 36 months, which again was similar to the periods of 24 and 42 months calculated, respectively, for Thailand and north-eastern Australia (Wium-Andersen & Christensen 1978; Duke *et al.* 1984). In this study, leaves in the sun had a shorter lifespan than leaves in the shade, some of the latter having a recorded longevity of approximately 50 months.

In our study, flowering occurred during the summer months, which is in agreement with the observations of Saenger (1982) in central Queensland. The major appearance of flower buds followed the flush of leafing in December with a lesser appearance in late summer/early autumn. In Thailand and Australia a correlation was noted between vegetative and floral phenologies, in that depressed leaf production occurred when production of flowers and fruits was maximal. This investigation appears to provide evidence supporting the correlation in respect of bud development and flowering. As mentioned earlier, no propagules grew to maturity during the course of this study. The longest period that developing propagules remained on the trees was 8 months. Although some abscission of reproductive material was due to natural conditions, most loss was clearly the result of the high number of visitors to these trees. Mature propagules were recorded at an earlier period when there were few visitors.

Little information is available on floral phenology of *L. racemosa*. Our observations compare very well with those of Saenger (1982) and Duke *et al.* (1984) for Queensland. However, it appears that flowering and fruiting take place over a slightly longer period than in central Queensland (Saenger 1982), possibly indicating a relationship between reproductive behaviour and latitude.

Studies at Beachwood have indicated that mangrove litter makes a significant contribution of organic material to that ecosystem, of which more than 60% is leaf material (Steinke & Charles 1984). Consequently, vegetative phenology forms an important aspect of studies concerning production and utilization of organic material in the mangrove ecosystem (Wium-Andersen & Christensen 1978; Saenger & Moverley 1985). Leaf abscission rates provide a measure of the organic input to the system, whereas leaf emergence rates give an indication of the physiological state of the trees, in particular their productivity. The input of organic matter, particularly fallen leaf material, is significant, as it has been shown to form the basis for a complex estuarine food web (Odum & Heald 1972; Snedaker 1978).

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